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Impacts of invasive Australian acacias: implications for management and restoration

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ABSTRACT

Aim The biophysical impacts of invasive Australian acacias and their effects on ecosystem services are explored and used to develop a framework for improved restoration practices.

Location South Africa, Portugal and Chile.

Methods A conceptual model of ecosystem responses to the increasing severity (density and duration) of invasions was developed from the literature and our knowledge of how these impacts affect options for restoration. Case studies are used to identify similarities and differences between three regions severely affected by invasions of Australian acacias: *Acacia dealbata* in Chile, *Acacia longifolia* in Portugal and *Acacia saligna* in South Africa.

Results Australian acacias have a wide range of impacts on ecosystems that increase with time and disturbance, transform ecosystems and alter and reduce ecosystem service delivery. A shared trait is the accumulation of massive seed banks, which enables them to become dominant after disturbances. Ecosystem trajectories and recovery potential suggest that there are important thresholds in ecosystem state and resilience. When these are crossed, options for restoration are radically altered; in many cases, autogenic (self-driven and self-sustaining) recovery to a pre-invasion condition is inhibited, necessitating active intervention to restore composition and function.

Main conclusions The conceptual model demonstrates the degree, nature and reversibility of ecosystem degradation and identifies key actions needed to restore ecosystems to desired states. Control and restoration operations, particularly active restoration, require substantial short- to medium-term investments, which can reduce losses of biodiversity and ecosystem services, and the costs to society in the long term. Increasing restoration effectiveness will require further research into linkages between impacts and restoration. This research should involve scientists, practitioners and managers engaged in invasive plant control and restoration programmes, together with society as both the investors in, and beneficiaries of, more effective restoration.

Keywords

Acacia, biodiversity loss, biological invasions, degradation ecology, ecosystem functions, ecosystem services, impact mechanisms, invasive species, seed banks, soil nutrients.

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INTRODUCTION

Many invasive plant species are able to transform ecosystems (Richardson *et al.*, 2000; Ortega & Pearson, 2005), resulting in losses of biodiversity, altered ecosystem functioning and a changed capacity to provide services (Vitousek *et al.*, 1997; Pimentel, 2001; Levine *et al.*, 2003; Didham *et al.*, 2007; Pejchar & Mooney, 2009; Vilà *et al.*, 2010). Management interventions that address these impacts are underway in many parts of the world. They include measures to prevent introductions, efforts to detect and eradicate new invaders, biological control and various efforts aimed at mitigating impacts (Pyšek & Richardson, 2010; Wilson *et al.*, 2011). Many programmes adopt a passive approach to restoring invaded systems and simply aim to remove the existing invaders and limit or prevent their regeneration. This approach often fails to achieve the desired outcome of a functional ecosystem dominated by native species (D'Antonio & Meyerson, 2002; Hulme, 2006; Reid *et al.*, 2009; Blackwood *et al.*, 2010). Practical problems that prevent the achievement of goals include 'secondary invasions' – the rapid replacement of the removed invasive species by others that capitalize on disturbance caused by the control operations. Resource alterations caused by the invasive species, the management intervention or combinations of these also often complicate or thwart restoration efforts (Galatowitsch & Richardson, 2005; Buckley, 2008; Young *et al.*, 2009). 'Legacy effects' – long-lasting changes in ecosystem structure such as increased soil nutrient levels that persist following the removal of the invasive species – are another major problem (D'Antonio & Meyerson, 2002; Marchante *et al.*, 2009). The result is that many control and restoration efforts have unplanned and undesirable outcomes and do not achieve sustainable mitigation of the impacts caused by invasive species. We contend that better mitigation of impacts caused by invasive plant species demands an improved understanding of the interacting factors that generate such impacts, and recognition that control and restoration measures must explicitly address the fundamental drivers of such impacts and their effects.

At least 23 Australian *Acacia* species (a group of 1012 species in *Acacia* subgenus *Phyllodineae* native to Australia; see Miller *et al.*, 2011 for taxonomic details) are major or emerging invaders in many parts of the world (Castro-Díez *et al.*, 2011; Richardson & Rejmánek, 2011; Richardson *et al.*, 2011). They have a range of ecological and socio-economic impacts (Le Maitre *et al.*, 2000; De Wit *et al.*, 2001; Marchante *et al.*, 2003, 2008a,b; Gaertner *et al.*, 2009; Hellmann *et al.*, 2011; Marchante, 2011; Rascher *et al.*, 2011). The range and magnitude of the impacts of existing invasions are becoming more severe, and similar impacts are likely to emerge in other areas where invasive acacias were introduced more recently (Richardson *et al.*, 2011). Multifaceted interventions are needed to achieve effective control and restoration of ecosystems affected by such invasions. Restoration efforts have been carried out in several areas, with mixed results (Yelenik *et al.*, 2004; Holmes *et al.*, 2008; Marchante *et al.*, 2009; Marchante *et al.*, 2011a). We suggest that improved restoration demands clearer insights into the trajectories and processes leading to degradation or altered ecosystem functioning. We further propose that such improved insights can be developed by collating insights on Australian *Acacia* invasions from different parts of the world. This study therefore seeks to develop a conceptual understanding of ecosystem changes driven by invasive Australian acacias. We focus on three regions where problems are most acute and where most information is available. We review the impacts of acacia invasions, on both biophysical and ecosystem services, drawing on published information and the insights of the authors. We then develop a conceptual model linking degradation to restoration and apply this to Australian acacias based on case studies on three continents. By drawing out cross-continental similarities and differences, we synthesize insights to show how knowledge of the range and complexity of impacts can be used to direct restoration towards desired outcomes.

IMPACTS OF *ACACIA* INVASIONS ON BIOPHYSICAL FEATURES AND ECOSYSTEM SERVICES

This section addresses both the biophysical impacts (those which affect ecosystem structure and function) and ecosystem service impacts (those where the biophysical impacts also affect the generation and delivery of ecosystem services to society).

Invasive Australian acacias, like many other invasive species, have a wide range of impacts including a number that interact in a synergistic fashion (Fig. 1; specific impact studies summarized in Table S1). *Acacia* species have been shown to induce simultaneous changes in the above- and below-ground communities, microclimates, soil moisture regimes and soil nutrient levels (Fig. 1; Marchante *et al.*, 2003, 2008a; Yelenik *et al.*, 2004; Werner *et al.*, 2010; Gaertner *et al.*, 2011). Many changes are directly attributable to key traits of *Acacia* species: their rapid growth rates and ability to out-compete native plants (Morris *et al.*, 2011); their capacity to accumulate high biomass; large, persistent seed banks; and their capacity to fix nitrogen (Yelenik *et al.*, 2007). These features enable them to dominate competitive interactions with native species. Many of the abiotic changes and biotic responses to them are tightly linked and may advance simultaneously rather than sequentially (Hobbs *et al.*, 2009), as does the progression from structural to functional impacts (Fig. 1).

The impacts of Australian acacias on biodiversity and ecosystem properties and functions also affect the delivery of ecosystem services and the benefits that society derives from them. Ecosystem services include: supporting services (e.g. soil formation); regulatory services (e.g. water flow and nutrient cycling); production services (e.g. food and fibre); and cultural or life-enhancing services (e.g. recreation or educational opportunities to sustain human well-being) (Fig. 2; Table S1; Daily, 1997; Brauman *et al.*, 2007). Invasions by transformer species (*sensu* Richardson *et al.*, 2000) have marked effects on the factors that regulate ecosystem processes and their

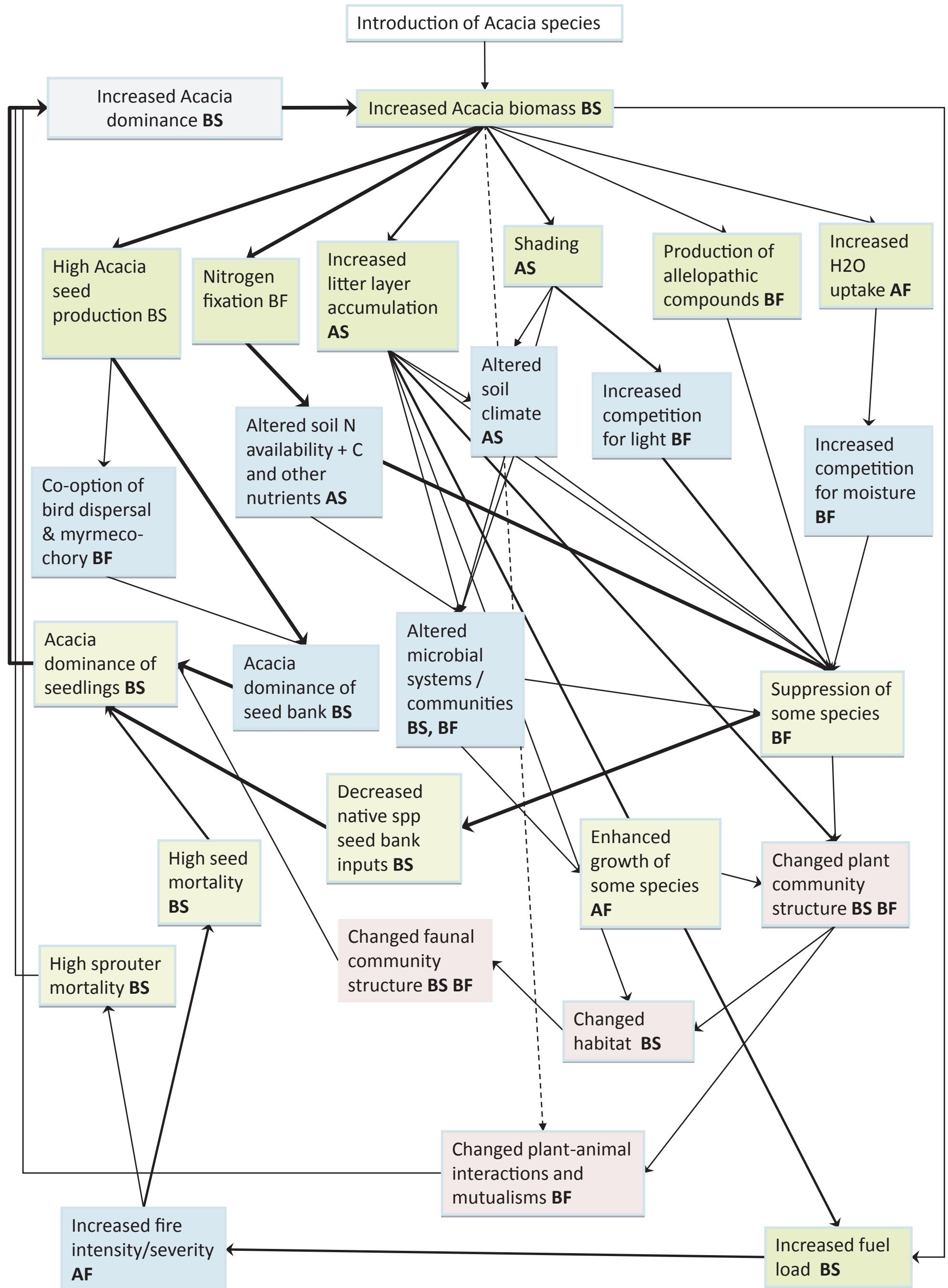

Figure 1 A cause-and-effect network diagram of the impacts of Australian *Acacia* species showing the pathways of the main mechanisms and their interactions. The width of the arrows indicates the relative importance of the pathways based on the literature (Table S1); the dotted arrow indicates a probable link. The mnemonics are composed as follows: B = biotic, A = abiotic, S = Structure and F = function. For more explanation, see the text, and for specific studies, see Table S1. Colours are included to simplify interpretation and indicate successions of cause and effect. We have omitted feedbacks and feed-forwards loops (e.g. between successive generations of invaders in fire-prone systems) because they become too complicated to include in a single diagram.

interactions (Chapin, 2003): resource supply, the modulating environment, disturbance regime, species interactions and human activities. These changes in ecosystem processes in turn alter the supply of corresponding ecosystem services (Pejchar & Mooney, 2009; Vilà *et al.*, 2010). The effects on supporting services propagate directly and indirectly through all the services (Kinzig *et al.*, 2007; Fig. 2). Regulating and cultural services are affected by the initial supporting service impacts. Provisioning services are altered by the changes in regulating services. While some services (e.g. wood supply) may be

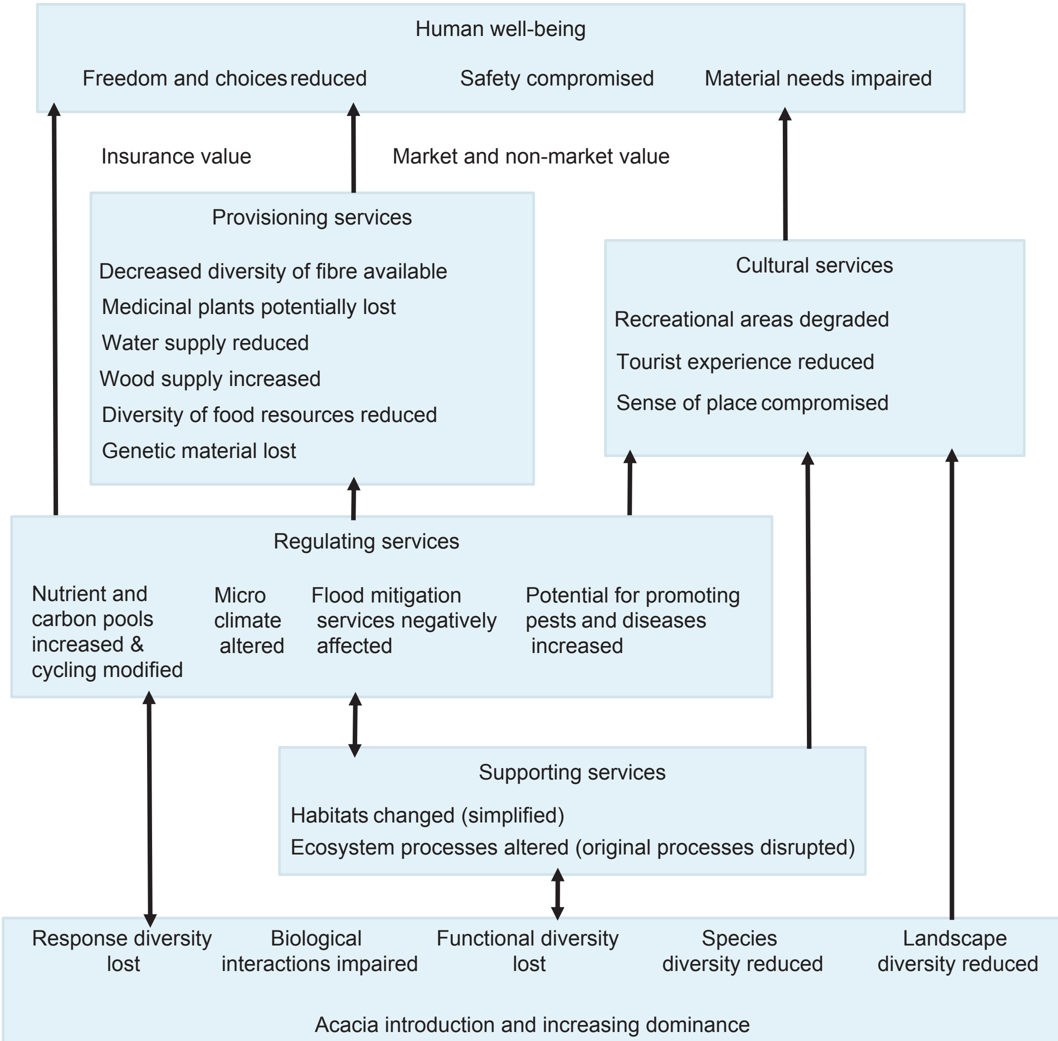

Figure 2 Conceptual model of the impacts of invasive Australian acacias on ecosystem services, illustrating how impacts on key elements of biodiversity and ecosystem structure and function propagate upwards to influence ecosystem services. Adapted from Kinzig *et al.* (2007).

enhanced by *Acacia* invasions, most provisioning services are negatively affected (Fig. 2, see also Fig. S1). Ultimately, human well-being is negatively affected by the overall changes in provisioning, regulating and cultural services, with decreases in the supply and diversity of available material, and safety and freedom of choices being compromised (Pejchar & Mooney, 2009).

There are many examples of impacts on ecosystem services and the benefits they provide (see Table S1). Riparian stands of *Acacia mearnsii* in South Africa use more water than adjacent dryland invasions by the same species or the native vegetation the invaders replaced (Dye *et al.*, 2001; Dye & Jarmain, 2004). The high biomass in dryland *Acacia* stands is directly related to their transpiration, and thus, the extent of reductions in river flows from invaded watersheds relative to the natural vegetation (Le Maitre *et al.*, 1996, 2000; Le Maitre, 2004). Invasions can therefore result in reduced availability of water to agriculture, industry, recreation, conservation and for domestic use, with significant implications for water security (Görgens & van Wilgen, 2004). The high biomass of *Acacia saligna* (and other acacia species) also leads to high fuel loads (van Wilgen & Richardson, 1985), which can increase the severity of fires, kill resprouting plants and seed banks and alter the soil structure and condition by burning the organic matter that binds soil particles, inducing water repellency (Fig. 1; Scott *et al.*, 1998; Van Wilgen & Scott, 2001; Holmes, 2001). This in turn adversely affects the soil stabilization and sediment regulation services and could increase river and dam sedimentation rates.

Although many invasive alien plants were introduced and are still used to deliver certain services and benefits (generally production, regulation or aesthetic services, Fig. S1; Kull *et al.*, 2011), the subsequent invasions usually have a detrimental effect on service supply (De Wit *et al.*, 2001; Van Wilgen *et al.*, 2008, 2011), and this has adverse impacts on the societies that depend on these services (Fig. 2; Pejchar & Mooney, 2009; Vilà *et al.*, 2010). Invasions have often led to conflicts of interest where the benefits of the goods and services provided by the species are accrued by one group of stakeholders, while the associated adverse impacts are borne by others (Van Wilgen *et al.*, 2011). For example, the benefits from the commercial use of *A. mearnsii* in South Africa for wood chips and tanbark (Griffin *et al.*, 2011) accrue to a relatively small group, while the costs of invasions are borne by a much wider group (De Wit *et al.*, 2001; Van Wilgen *et al.*, 2011). These conflicts are difficult to resolve when proposing control or containment measures and when motivating for restoration of natural ecosystems. The complexity of these conflicts makes a strong case that societal support for management, and restoration of affected ecosystems should be based on a thorough understanding of the impacts on services and benefits that society derives from those ecosystems (D'Antonio & Meyerson, 2002; Clewell & Aronson, 2006; Turpie *et al.*, 2008; Aronson *et al.*, 2010). Such deconstruction facilitates the objective evaluation of particular services, thus paving the way for resolution of conflicts of interest.

DEGRADATION AND RESTORATION POTENTIAL – THE ELUSIVE LINK

Restoration solutions have tended to be context specific, but a growing body of research seeks to provide broadly applicable strategic frameworks that recognize strong links between an understanding of the ecological responses to ecosystem degradation and linked options for restoration (Holmes & Richardson, 1999; Suding *et al.*, 2004; Holmes *et al.*, 2005; King & Hobbs, 2006; Miller & Hobbs, 2007; Temperton, 2007; Bascompte, 2009; Hobbs & Richardson, 2011). We draw on elements of these frameworks in the present study.

Practical experience and experimental manipulations suggest that the likelihood of successful passive restoration (through autogenic recovery) decreases rapidly as the intensity and/or duration of the perturbation increases, but not necessarily linearly (Milton *et al.*, 1994; Whisenant, 1999). Degradation and restoration can be conceptualized as continuous responses punctuated by stepwise changes as one or more thresholds are crossed (Fig. 3; Suding *et al.*, 2004; King & Hobbs, 2006). As degradation progresses, the effects of the driving factors initially become evident through changes in biotic structure (e.g. species abundance, initial stage), then the ecosystem may pass a threshold following a disturbance that leads to changed abiotic structure (e.g. soil structure) and lastly crosses a second threshold that becomes evident through changes in functional components (e.g. disturbance regimes) and resource loss (King & Hobbs, 2006). These changes initiate feedbacks via biotic and abiotic components and their interactions, resulting in further degradation as long as the drivers of change operate. Initial changes in biotic structure (initial stage, Fig. 3) may often be reversed without significant intervention although some manipulation of native plant community structure (e.g. species re-introductions) may be necessary. Changes in abiotic structure and function are more challenging to reverse, especially where key processes have become non-functional or ecosystem thresholds have been passed (post-disturbance or after protracted impacts, Fig. 3; Groffman *et al.*, 2006; Hobbs *et al.*, 2009). The same general model can be applied to invasions by alien plants (Brooks *et al.*, 2010), including acacias (Gaertner *et al.*, 2012). We apply this conceptual model to case studies across three continents highlighting the links between degradation and restoration (Boxes 1–3).

Synthesis of cross-continental similarities and differences

The three case studies of *Acacia* invasion share some important drivers of change: the triggering of invasion by fire (or other disturbance), production of large, long-lived seed banks, increased soil nitrogen, suppression of native vegetation and eventual depletion of native seed banks and reduced restoration potential (Fig. 1, Boxes 1–3). *Acacia* invasions in South African fynbos and Portuguese dune systems have the most similar invasion trajectories and impacts, perhaps because the species studied, *A. saligna* and *Acacia longifolia,* respectively, have similar growth forms and canopy structures, which create functionally similar environments in dense stands. Both ecosystems have nutrient-poor, deep, sandy soils and support shrubland vegetation. In contrast, the invasions in Chile are in taller forest and riparian vegetation on floodplains, where soils vary from rich clay soils to poorer, sandy soils. In South Africa and Portugal, invasion results in increased biomass and litter layers, rapid species displacement following fire and changed decomposition processes. In Portuguese coastal systems (Marchante *et al.*, 2008b) and lowland fynbos (Yelenik *et al.*, 2004), the soil organic matter and leaf litter layer increased, resulting in higher soil moisture levels following invasion. By contrast, in Chilean forest, soil moisture levels decreased following *Acacia* invasion.

The progression of invasion stages is strongly linked to fire cycles; for example, in fynbos, three fire cycles (a total average time-span of 45 years) drive a change from natural shrubland vegetation with scattered *Acacia* trees to a dense *Acacia* woodland with depleted native seed banks (Box 1). In fynbos, fire stimulates germination in both native and *Acacia* seed banks, whereas in Chilean forest and Portuguese dunes, fire promotes *Acacia* recruitment more than the native species. Fire is a key ecosystem process in fynbos, but it is less important in Portuguese dune systems except in the interior. Fires were rare or exceptional in Chilean forest ecosystems prior to human settlement but have become frequent following the establishment of extensive plantations of pines and eucalypts.

There are also differences that appear to be unique to the particular ecosystem that is invaded and merit further research. For example, in Chile, a light-demanding native forest species did not survive under closed *Acacia* stands, while other more, shade-tolerant species survive underneath these *Acacia* stands but show very limited growth (Box 3; Fuentes-Ramírez *et al.*, 2011). In fynbos ecosystems, native seed banks persisted for

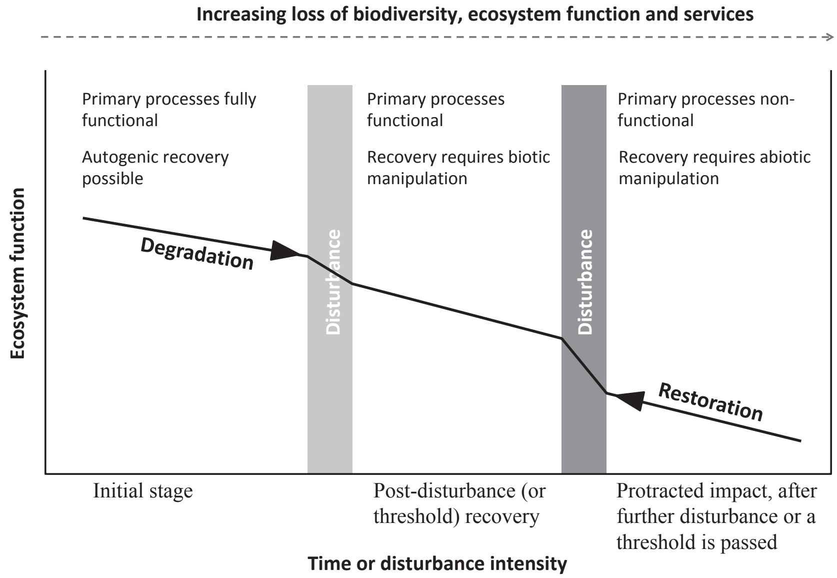

Figure 3 Conceptual model of ecosystem degradation and thresholds (vertical bars) in key ecosystem process, which determine the responses of the system to release from the pressures driving degradation (adapted from King & Hobbs, 2006 and Gaertner *et al.*, 2012). We recognize three stages separated by thresholds marked by disturbances or other factors. The initial stage where the system is able to recover autogenically; post-disturbance recovery where the biota has changed and restoration requires biotic manipulation; and protracted invasions, sometimes following further disturbances, where ecological process has collapsed and requires abiotic manipulations to restore them.

one fire cycle longer following dense *A. saligna* invasion in mountain fynbos than in lowland fynbos on deeper sands (Holmes, 2002). In disturbed lowland fynbos, fossorial mammals are particularly abundant and can inhibit native species recovery following *Acacia* removal (Box 1; Holmes, 2008).

Similar ecosystem-specific invasion impacts have also been shown in other studies. For example, in native forests, in South Africa, the biomass impacts of *Acacia melanoxylon* invasion may cause little or no change in structure and may facilitate the regeneration of some forest tree species (Geldenhuys, 1986, 1996). In Chile, however, although there was some recruitment and persistence of shade-tolerant native forest species, this did not lead to forest re-establishment (Box 3), suggesting that knowledge of ecosystem types does not necessarily allow the prediction of effects. Thus, an understanding of both regional native ecosystem dynamics and localized invasion dynamics is needed to guide effective restoration. However, the development of a broader understanding, such as the cross-continental comparisons made here, can complement this by guiding localized studies to determine which of the generic impacts are likely to be at play in different situations.

Trajectories of *Acacia* invasion, thresholds and their implications for restoration

Effective restoration requires an understanding of the drivers and dynamics that have resulted in ecosystem modification (Richardson *et al.*, 2007; Holl & Aide, 2010). The first step should be to evaluate the degree to which the ecosystem has been altered by the invasion and whether biotic or abiotic thresholds have been crossed. The conceptual model and case studies presented here suggest that fire history, seed banks, leaf litter and soil characteristics should be assessed as they play a significant role in some invasions by Australian acacias and provide important pointers for ecosystem restoration strategies (Fig. 3, Boxes 1–3). The type and degree of alteration depends on the traits of the invasive species and on the ecosystem invaded (see Impacts of *Acacia* invasions on biophysical features and ecosystem services section above) and are key determinants of the restoration requirements and outcomes (see Table S2 for a summary of specific studies). In South African fynbos invaded by *A. saligna*, fire is the primary driver of change (Box 1). Recruitment of native seedlings is reduced by the depletion of native seed banks and competition from the abundant *Acacia* seedlings. A threshold for autogenic recovery will be passed if, after subsequent fire cycles, *Acacia* species dominate the community, and the native seed bank is depleted. In Portuguese coastal dunes, biotic changes follow a similar pattern; however, despite impoverished native seed banks and a dominance of *A. longifolia*, the native ecosystem is still able to partially recover autogenically. This suggests that degradation thresholds have been crossed, but with active restoration, such as the introduction of native species or removal of litter, the system may recover.

In both dune and fynbos ecosystems, soil enrichment by nitrogen-fixing *Acacia* species can result in herbaceous species becoming dominant after *Acacia* control. Higher soil N (which may facilitate both nitrophilous species and the acacias themselves) and thick litter layers may further hamper restoration and may need to be mitigated for the system to fully recover, suggesting that abiotic thresholds have also been crossed in some situations.

Box 1 Case study: *Acacia saligna* invasion in South African fynbos – driven by fire and competitive ability (faster growth rate, greater biomass and rapid accumulation of a persistent soil-stored seed bank)

Acacia saligna was widely planted for drift sand control and tannin production following its introduction to South Africa's Cape Floristic Region (CFR) in the 19th century. It has since spread to form extensive dense stands, particularly in lowland fynbos. Stand expansion and densification are driven by fire, as the tree resprouts and its seeds require a heat pulse to germinate (Jeffery *et al.*, 1988). The tree produces large numbers of long-lived, hard-coated seeds that can remain dormant in the soil (Milton & Hall, 1981), and seed banks in excess of 40,000 per m^2 have been recorded (Holmes *et al.*, 1987).

Small mammals can consume all the seed of scattered trees, but seeds are also removed by ants that take them below ground in their nests, safe from predation. These native ants have probably been a major vector in the establishment of dense stands (Holmes, 1990). During initial invasion, native fynbos richness (F) and seed banks (E) remain relatively unaffected. Disturbance by fire triggers germination in fynbos and *A. saligna*, but *A. saligna* quickly outgrows the fynbos in the post-disturbance recovery stage to form tall, dense stands (A) that exclude the shorter fynbos and no longer provide suitable habitat for small mammals. This leads to a rapid accumulation of the *Acacia* seed bank in the soil (C). The time-scale for each invasion stage links strongly to the fynbos fire cycle, which averages 15 years (range 4–40 years).

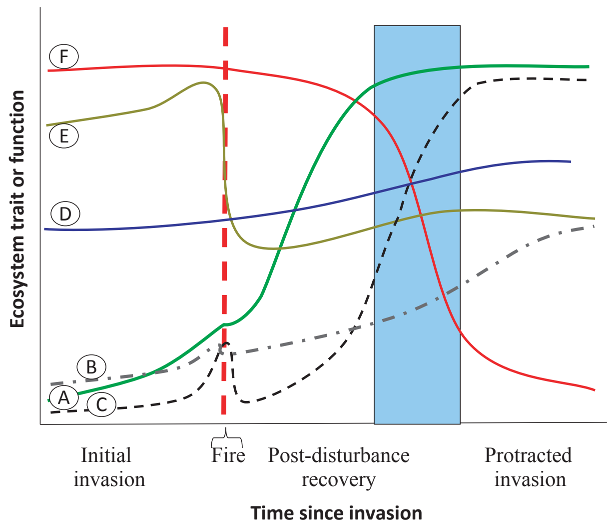

Figure Box 1 Trends in key drivers and ecosystem responses to different stages of *A. saligna* invasions in South African fynbos: (A) *Acacia* density, (B) soil nitrogen, (C) *Acacia* seed bank, (D) soil moisture availability, (E) native seed banks and (F) native species richness. The dashed vertical line represents a disturbance event; in this case, fire that results in a threshold being crossed. The box indicates the vicinity of the threshold to protracted invasions.

After a fire, in the newly formed, dense *Acacia* stand (A), fynbos seed banks persist in the soil at lower densities (E; Holmes, 2002); following a subsequent fire, these will germinate alongside the *Acacia* seeds and fail to establish. The higher soil nutrient status (B) in *Acacia*-invaded fynbos (Musil & Midgley, 1990) does not hamper fynbos seedling growth; rather, the seedlings are outnumbered and outgrown by the acacias (Musil, 1993). *Acacia saligna* has a faster growth rate than a native shrub (*Protea repens*) and out-competes it when grown in mixture (Witkowski, 1991). Fire is the primary driver of change. With each subsequent fire cycle, *A. saligna* becomes increasingly dominant, and the fynbos seed banks more depleted, with a concomitant reduction in autogenic restoration potential (Holmes and Cowling, 1997a,b). There is a slight increase in surface soil moisture content (D) in dense stands, probably linked to the increase in soil organic matter (Yelenik *et al.*, 2004).

Once the severity of the invasion exceeds the threshold for autogenic (self-sustaining) recovery, control of *Acacia* results in herbaceous species becoming dominant (e.g. grasses *Cynodon dactylon*, *Ehrharta calycina,* and alien annuals) (Holmes, 2008). This change to an alternative stable state is supported by the abiotic changes (higher soil nitrogen levels that promote the competitive grasses; Yelenik *et al.*, 2004) and maintained by a positive feedback loop with fossorial mammals (Holmes, 2008). The fossorial mammals increase in density and activity in grass-dominated ecosystems and create an extremely hostile environment for fynbos re-establishment. Re-introduction of native species must be preceded by small mammal control, either directly, or indirectly through the removal of grasses using herbicide and fire. To pre-empt the dominance of herbaceous species after clearing *A. saligna*, missing guilds such as long-lived native shrubs and restioids should be re-introduced, preferably by seed following a summer management burn.

Successful restoration of *Acacia*-invaded systems needs to include follow-up treatment as all invasive *Acacia* species accumulate persistent soil seed banks across a range of ecosystem types. Both *A. saligna* and *Acacia dealbata* (*A. longifolia* less so) resprout after cutting; it is thus important to use herbicide in the control treatments. If the native seed bank is depleted (biotic threshold crossed), re-introduction of native species through either planting or sowing is required to restore ecosystem structure. In South African fynbos and Portuguese dunes, fire can be used to facilitate litter removal and to reduce

Box 2 Case study: *Acacia longifolia* invasion in Portuguese coastal dunes (Nature Reserve of São Jacinto Dunes – NRSJD) – driven by fire, biotic and abiotic changes

Acacia longifolia was widely planted to stabilize Portuguese coastal dunes between the 1890s and 1940s. Stimulated by fires, it has spread to form extensive dense stands that progressively transform the original vegetation, characterized by a low plant cover (herbs, few shrubs and trees), to continuous stands dominated by *A. longifolia* (Marchante *et al.*, 2003; Marchante, 2011; Rascher *et al.*, 2011).

While the density of *A. longifolia* (A) in NSJRD is still low, the cover of native plants decreases, but native species richness (F), native seed banks (E), water content at soil surface (D) and total nitrogen (B) are not significantly affected. Many long-lived *A. longifolia* seeds are produced (over 12,000 per m^2 per year), accumulating up to 1500 seeds per m^2 in the soil seed bank (C) after a few decades (Marchante *et al.*, 2010). Immediately after a fire, the density of *A. longifolia* (A) and native species richness (F) are greatly reduced; total nitrogen (B) may decrease, depending on fire intensity. *Acacia longifolia* quickly recolonizes, mainly through the germination of seeds, initially partially depleting the seed bank (C) but rapidly replenishing it. As *A. longifolia* reaches maturity, it rapidly reaches > 80% cover, out-competes native species and accumulates a thick litter layer.

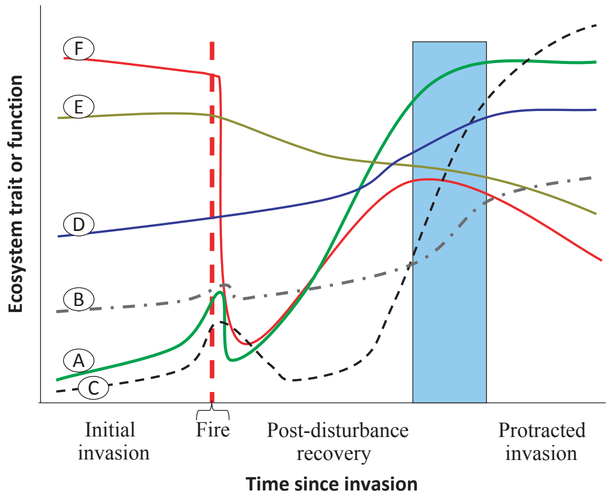

Figure Box 2 Trends in key drivers and ecosystem responses to *A. longifolia* invasions in Portuguese sand dune systems: (A) *Acacia* density, (B) soil nitrogen, (C) *Acacia* seed bank, (D) soil moisture availability, (E) native seed banks and (F) native species richness. The dashed vertical line represents a disturbance event; in this case, fire that results in a threshold being crossed. The box indicates the vicinity of the threshold to protracted invasions.

The native seed bank (E), which persists when *A. longifolia* is present for short periods and/or at low densities (Marchante *et al.*, 2011b), decreases after fire owing to seed germination or destruction. As the invasion becomes protracted, native species cover decreases even more although native species richness (F) is sustained for much longer because some species persist at low densities (Marchante *et al.*, 2003; Marchante, 2011). In these nutrient-poor sand dunes, soil carbon and nutrients, especially total nitrogen (B), progressively increase after invasion, but these increments only become evident after protracted invasion (i.e. several decades), although microbial processes and mineral nitrogen are affected much earlier (Marchante *et al.*, 2008a,b). Soil water content (D) increases after *A. longifolia* invasion as a result of increases in soil organic matter and leaf litter accumulation compared with the native state, which is characterized by bare sand and low native species cover (Marchante *et al.*, 2008a).

As the invasion becomes protracted, the autogenic recovery potential of invaded areas decreases: native seed banks (E) become more impoverished (Marchante *et al.*, 2011b), reinvasion potential (acacia seed bank, C) increases (Marchante *et al.*, 2010) and soil carbon and nutrients, especially nitrogen (B), become and remain high for long periods (Marchante *et al.*, 2009). Autogenic recovery after removal of *A. longifolia* is slow with only partial recovery after 6 years (Marchante *et al.*, 2009, 2011a) suggesting that full autogenic recovery may not be possible. Nevertheless, generalist plant species rapidly colonize the cleared areas and are slowly replaced by some characteristic dune species, with some native legume species growing better in invaded soils (Rodríguez-Echeverría *et al.*, 2009). These results suggest that ecosystem thresholds may have been crossed, but the system may recover with active restoration. In areas invaded for protracted periods, removal of the nitrogen-rich, slow-decomposing litter layer facilitates ecosystem recovery, both biotically (plant and microbial communities) and abiotically (soil nutrients) (Marchante *et al.*, 2004, 2009, 2011a), as well as reducing the *A. longifolia* seed bank (Marchante *et al.*, 2010). Other active restoration practices namely transplanting of native species and use of moderate fire to facilitate litter removal and simultaneously deplete *A. longifolia* seed bank may also help to restore invaded ecosystems. Follow-up control of *A. longifolia* and other alien invasive species is essential to sustain recovery of native ecosystems (Marchante *et al.*, 2010).

Acacia seed banks. In South African fynbos, fire provides the necessary germination cues (including heat pulse and smoke treatment) to stimulate native species recovery provided that fuel loads are appropriate. In Portuguese dunes and Chilean forests, this strategy should be carefully planned and used as a compromise as it may reduce native seed banks.

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Box 3 Case study: *Acacia dealbata* invasions in Chilean woodlands and forests – driven by disturbance and competition

Acacia dealbata was introduced to Chile for ornamental purposes, and invasions currently extend from Los Lagos in the south to Valparaiso in the north. The species occurs in riparian habitats, roadsides and heavily disturbed areas (Pauchard & Maheu-Giroux, 2007).

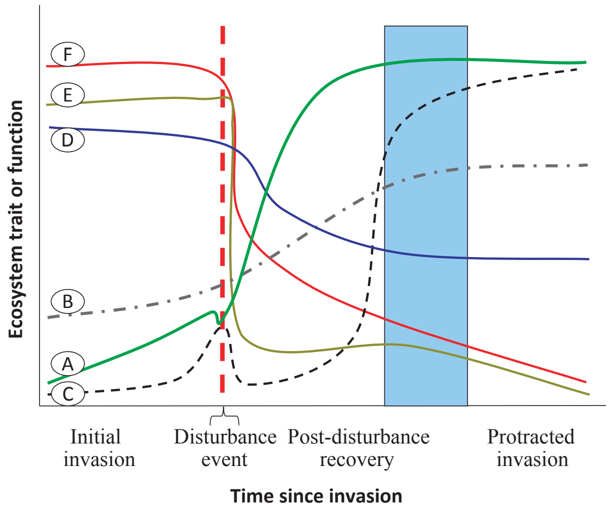

Figure Box 3 Trends in key drivers and ecosystem responses to *A. dealbata* invasions in Chilean native forest. (A) *Acacia* density, (B) soil nitrogen, (C) *Acacia* seed bank, (D) soil moisture availability, (E) native seed banks and (F) native species richness. The dashed vertical line represents a disturbance event, often a fire, which results in a threshold being crossed. The box indicates the vicinity of the threshold to protracted invasions.

In Chilean native forests, the trends during initial invasion are similar to those in the other case studies. Disturbance (such as fire or clear cutting) depletes native seed banks and reduces native species cover, opening up space that *A. dealbata* rapidly colonizes. During post-disturbance recovery, the acacias rapidly increase their density (A) through epicormic resprouting, out-competing native species (F), increasing soil nitrogen (B), accumulating large seeds banks (C) and decreasing available soil moisture (D). After protracted invasions, an alternate stable state is reached, which is similar to that in the fynbos with *Acacia* dominance and little or no forest recruitment. In Chile, fire promotes the spread of *A. dealbata* by reducing native species cover and stimulating epicormic sprouting. Fire may also reduce native seed viability and stimulate germination of *Acacia* (a positive feedback loop). Native forest species abundance and cover is markedly lower under *Acacia* canopies (Fuentes-Ramírez *et al.*, 2010). Experiments on native species recolonization found that survival is poor and is only successful if the *Acacia* canopy is opened up, suggesting that light and possibly soil moisture are limiting recovery of some forest species (Fuentes-Ramírez *et al.*, 2011).

Acacia dealbata is particularly invasive in Chile because of its phenotypic plasticity; its high capacity for resprouting after fire and clear cutting; its allelopathic properties; and its rapid response to anthropogenic disturbances (Fuentes-Ramírez *et al.*, 2011). The species is heavily used for firewood when near human settlements, but clear cutting and fire promote resprouting, increasing the rate of expansion across the landscape. Forestry companies have become aware of the threat this species poses to protection zones in their plantations and are considering strategies to reduce its dispersal and restore invaded areas. However, there is still no unified effort to restore invaded areas, and impoverished rural communities still consider this species an important resource.

The success of a restoration strategy may depend on the control method applied to remove the invasive acacias. For example, in a study of dense *A. mearnsii* removal from fynbos riparian zones to increase river flows, restore sediment regulation processes and aquatic and riparian ecosystems, different results were noted for different control methods. Autogenetic recovery was found to be possible in 97% of *A. mearnsii* invasions provided that a ‘Fell & Remove’ treatment was used (Blanchard & Holmes, 2008). Removal of the felled *Acacia* material from the riparian zone without burning resulted in the best recovery because this allowed native species to recolonize from the soil seed bank and from propagules washed downstream. By contrast, in some areas that were felled and burnt, severe fires killed native seeds and resulted in very dense *Acacia* recruitment. This necessitated a follow-up foliar herbicide treatment that killed both *Acacia* and native dicotyledonous seedlings, resulting in a grass-dominated, weedy community. These complexities in ecosystem response to restoration activities demonstrate the need for ecological research to guide scientifically based strategies. Generalities are apparent, such as recognizing the initial biotic threshold. However, the specific context still needs to be taken into account and understood by checking for common impacts such as abiotic soil changes.

Effective restoration is never simple. Even after ‘apparent success’ in control of the trees, seeds of most *Acacia* species can lie dormant in the soil for decades (Milton & Hall, 1981; Pieterse & Cairns, 1988) and can hamper restoration following subsequent disturbance events such as fire. In this case, follow-up action and biological control can play key roles in the

Box 4 Priorities for research

1. Cross-continental research on invasions by *Acacia* species in analogous systems to identify and confirm commonalities and differences in the impacts and ecosystem responses, and to develop an understanding of their relationships to the driving factors behind the impacts.
2. Similar cross-continental comparisons of autogenic recovery following *Acacia* removal (at each stage in the invasion process). This research should aim to identify thresholds to autogenic recovery in different native ecosystems, and their links with transitions to alternative states, and relate them to ecosystem traits and drivers to provide an evidence base for restoration strategies and actions.
3. Effective ways to deal with the massive, long-lived seed bank and mass regeneration potential of acacia species, while facilitating native species recovery, and for managing raised soil nitrogen and accumulated litter.
4. Developing innovative management approaches and linked research to promote the restoration of resilient, multifunctional landscapes where invasive Australian *Acacia* species have created novel but ecologically and socially undesirable states (see Seastedt *et al.*, 2008).
5. Research into effective ways of actively involving society (individuals to institutions) in controlling invasive species and restoring ecosystems to conserve biodiversity, rebuilding functioning ecosystems and maintaining ecosystem services.

integrated management of the *Acacia* species and long-term restoration (Richardson & Kluge, 2008; Wilson *et al.*, 2011). Development of more effective measures for control and restoration will require closer collaboration between those studying the impacts and those attempting to restore the affected systems, because the interactions are complex and often not observable. Responses to control treatments can alter recovery pathways in ways that make restoration more difficult and intensive, providing a strong argument for involving restoration specialists in the planning of control measures. Restoration specialists can also help to design the research into impacts so that it addresses the causes of changes in ecosystem states and responses that dictate, for example, whether an autogenic recovery or active restoration strategy is adopted. We have outlined some priorities for research in Box 4.

Motivating for active restoration

We have described how invasive *Acacia* species trigger biophysical changes and altered biodiversity, ecosystem functioning and ecosystem service delivery and the implications of these changes for successful restoration. We have also emphasized that active restoration will be required to restore ecosystems following protracted invasion as they are unlikely to recover autogenically. Ideally, information about the ecological and societal consequences of invasions should result in investments in control and restoration, but this is rarely the case in practice. The emerging evidence of impacts should be used to engage society in dialogue about the costs and benefits of control and restoration and gain their support for such investments.

There is a growing recognition that we live in a world with finite natural resources and that we need multifunctional landscapes, which simultaneously protect biodiversity, preserve ecological functions, provide a range of ecosystem services and fulfil a variety of human needs (O'Farrell & Anderson, 2010). Invasions by acacias and other species pose a significant threat to the ability of those landscapes to meet such needs, and this threat needs to be addressed. Restoration requires the investment of substantial resources, so preventing or containing invasions early on is vastly preferable; however, there are many situations where clearing and restoration are justifiable in long-invaded areas (Wilson *et al.*, 2011). Options for reducing the direct investments include tailoring incentives for restoration to consider the extent of invasion, impact intensity (Holmes & Cowling, 1997b), perceived costs and benefits of invasive *Acacia* (Shackleton *et al.*, 2007; Kull *et al.*, 2011) and perceived value of ecosystem services (Turpie *et al.*, 2008; Bryan *et al.*, 2010) as well as seeking economies of scale (see Appendix S1).

The mismatch between management units and ecological process boundaries, and the involvement of diverse stakeholder groups, creates organizational challenges for rehabilitating landscapes (Briggs, 2001; Postel & Thompson, 2005; Hein *et al.*, 2006). Coordination of local-scale actions with regional conservation planning can be aided by spatially mapping social factors (Knight *et al.*, 2010; O'Farrell *et al.*, 2010), the value of ecosystem services (Dutton *et al.*, 2010) and impacts from invasive *Acacia* species (Van Wilgen *et al.*, 2008). This can help to prioritize areas for restoration, which will yield the greatest return on investment and where stakeholders have higher incentives and willingness to support restoration (Appendix S1; Chen *et al.*, 2010). Incentives for restoration can be increased within organized stakeholder groups through effective communication about how ecosystem services are affected by *Acacia* species (Briggs, 2001; Aronson *et al.*, 2010) and by providing alternative restoration options that result in similar landscape functions (Opdam *et al.*, 2006). This will require restoration practitioners to demonstrate much more effectively and quantitatively how their work results in the restoration of ecosystem services (Aronson *et al.*, 2010).

CONCLUSIONS

Millions of dollars are invested in the control of invasive alien species worldwide, including Australian acacias, and this expenditure will increase in the future. Many control efforts simply aim to remove the invader, giving insufficient consideration to the impacts of invasion and the longer-term outcomes of the control efforts. In many cases, the original invader may reinvade or a new species may invade the area. A thorough understanding of the factors driving the invasion and the changes in the biotic and abiotic components of the ecosystem can be used to direct control and restoration efforts. Insights into the potential thresholds, and the alternative ecosystem states that occur, can assist restoration practitioners in determining whether autogenic recovery is likely or whether active restoration is required. Successful restoration also relies on a sound understanding of social and ecological considerations.

We have used invasions by Australian acacias to demonstrate how invasion ecology and restoration ecology research can be combined to guide control and restoration. Research across three continents has found evidence that suggests that a key threshold is the state of the seed banks of native species. The importance of increases in soil nutrients varies between studies [e.g. crucial in the South African example (Box 1), but relatively unimportant in the Portuguese example (Box 2)], and high nutrient levels have been shown to sometimes facilitate reinvasion or secondary invasions. Fires can play a critical role where invasion radically increases fuel loads and can result in severe fires that damage soils, kill native resprouting species and deplete seed banks, thus inhibiting autogenic recovery.

Controlling invasive alien plants is generally very costly and requires sustained investment over long periods of time, particularly when dealing with species that have very large and long-lived seed banks, like many acacias. Active restoration adds additional expenses but can be effective in reducing the long-term costs of follow-up and maintenance operations. Biological control can also be an effective way of reducing the costs of control, restoration and follow-up operations (Wilson *et al.*, 2011). Such investments can only be justified when rigorous studies provide sound evidence that will assure stakeholders that the benefits of restoration outweigh the costs. Conflicts of interest are difficult and complex to resolve (Kull *et al.*, 2011), but a thorough assessment of the full socio-economic and environmental costs and benefits can be the catalyst for solutions that satisfy the majority of stakeholders (Van Wilgen *et al.*, 2011). Authorities need to put policies, legislation and incentives in place to guide public and private investment in controlling invasive alien plant species and combine this with passive or active restoration as required. Ultimately, the responsibility for progress in this area relies on invasion ecologists, managers of control operations and restoration practitioners finding ways to work together, learn from each other and put that knowledge into practice.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 A diagram showing the progression from biophysical impacts to ecosystem service impacts.

Table S1 Summary of the literature on the impacts of *Acacia* invasions on ecosystem structure and function and on ecosystem services.

Table S2 Summary of the literature on the impacts of invasions and the remedial measures needed for successful restoration.

Appendix S1 Financing restoration – Payments for Ecosystem Services.

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BIOSKETCH

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Author contributions: D.L.M. & D.M.R. conceived the idea for the study. D.L.M., M.G., E.M., E.-J.E. and A.P. submitted abstracts for inclusion in the *Acacia* workshop that generated the papers in this special issue. They, R.B., A.R., P.H. and D.M.R., participated in the workshop. All authors contributed to the section and Table S1 on biophysical impacts. D.L.M., P.O'F. and R.B. drafted the section on ecosystem service impacts, Figs 1 and 2 and Fig. S1. M.G., E.M., P.H., A.P., E.-J.E., A.R. and D.M.R. contributed to the section on restoration, Case studies and Table S2 on restoration. A.R. produced the initial version of Fig. 3 and revised it in collaboration with D.L.M., M.G., E.M., P.H., A.P. and E.-J.E. J.B. contributed to the text on motivating for restoration and the box on options for funding invasive alien plant control and restoration (Appendix S1). All authors contributed to the writing of the paper.

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